OSMIA (HYMENOPTERA: MEGACHILIDAE) DIVERSITY AT A SITE IN CENTRAL COASTAL CALIFORNIA

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Abstract.—Thirty species of the megachilid bee genus Osmia were recorded at a research reservation in central coastal California during two survey periods: 1937–43 and 1987–92. Diversity remained constant at 23 species between surveys. However, cumulative diversity increased from 23 to 30 species. The total number of species at this geographic locale is relatively high when compared with nine other surveys but is most typical of diversities found at other montane, midelevation latitudes. Differences between study periods suggest that long-term surveys are required to accurately assess species diversity.

Key Words.—Insecta, Hymenoptera, Megachilidae, Osmia, species diversity.

Studies of biodiversity often rely upon knowing numbers of species, information that is critical to testing some of the most frequently discussed hypotheses in basic and applied ecology, including island biogeography and species/area relationships (reviewed in Williamson 1981, MacArthur & Wilson 1967). Within the Apoidea, taxonomic summaries for broad geographic regions have been assembled (Michener et al. 1994, Ayala et al. 1993, Roubik 1989, Westrich 1989a & b, Rust et al. 1983, Tepedino 1982, Michener 1979, Moldenke 1976, Stephen et al. 1969), but fewer studies seek to determine local species diversity in preserved, natural settings (e.g. Thorp et al. 1994, Thorp & Gordon 1992, Ayala 1988, Rust et al. 1985).

We surveyed such a region for the solitary bee genus *Osmia*. This group represents the fifth largest genus of bees in North America, containing approximately 130 species (Rust 1974). Like other genera in the family Megachilidae, many species use pre-existing cavities in their environment for nesting. This trait makes them amenable to studies that use artificial nesting sites, including trap-nests (Krombein 1967). The present study concerns collections made by hand during two historical periods and at a single locale, the Hastings Natural History Reservation (Hastings). Our objectives were two-fold. First, we wished to gain a relatively complete record of *Osmia* species at a preserved site in California. Secondly, we wanted to compare collection results from two survey periods (1937–43 and 1987–92) for differences.

MATERIALS AND METHODS

Study Site.—The Hastings Natural History Reservation (Hastings) is located 42 km SE of Carmel in the Santa Lucia foothills of Monterey County, California (36°23′ N, 121°33′ W). Hastings is part of the University of California Natural Reserve System and is managed through the Museum of Vertebrate Zoology (U.C. Berkeley). It originally encompassed 664 ha. of land when established in 1937

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and currently covers 914 ha., ranging in elevation from 467–953 m (Griffin 1988). Griffin (1974, 1990) describes six major plant communities at Hastings with 90 of the 576 plant species (15%) being introduced (Knops et al. 1995).

Early research at Hastings was directed by the resident zoologist Jean M. Linsdale who helped to accumulate a wealth of information on the natural history and species composition of the reserve (Linsdale 1947). Several taxonomic surveys were produced, including an extensive insect collection made by C. D. Michener in the late 1930s. The rediscovery of a portion of this collection in metal storage cabinets during the late 1980s coincided with our efforts to survey bee species at Hastings and other California sites (Thorp et al. 1992). Here we compare *Osmia* diversity at Hastings between the two survey periods as well as its overall diversity to other North American surveys.

Collections were made primarily with a hand-held insect net with the date recorded for each specimen. Some specimens collected during the early survey period (1937–43) were stored in gelatin capsules and held in glassine envelopes with labelled, 7.6 cm × 21.7 cm index cards. These latter specimens were later mounted on insect pins to facilitate species determination. Other specimens from that period were deposited in the Snow Entomology Museum (SEM) at the University of Kansas. These specimens were re-examined for this study and later redeposited at SEM. Specimens from the most recent survey will be deposited at University of California (Berkeley and Davis campuses) entomological museums.

Host plant associations were recorded for specimens during both survey periods, but most often during the second one. When possible, pollen sources were determined by observation of foraging female bees and microscopic comparison of pollen taken from flower and bee specimens.

RESULTS AND DISCUSSION

A total of 377 Osmia specimens were collected during the first survey period (1937-1943). Most (360) were collected during 1938 with only four specimens from 1939, 12 from 1940 and one from 1943 (none in 1937, 1941 and 1942). During the 1987–92 period, 602 Osmia specimens were collected, most of these during the last two years of the study, 1991 (227) and 1992 (222); fifteen specimens were collected during 1987, none during 1988, 52 during 1989 and 86 during 1990. During both survey periods, 23 Osmia species were documented. Seven species were unique to each survey, with a total of 30 species overall (Table 1).

Geographic Comparisons of Diversity.—Osmia species diversity at Hastings is relatively high. The 30 species collected there represent over 20% of the 130 species estimated for North America by Rust (1974) and 10 of the 12 subgenera (excepting Diceratosmia and Nothosmia). Despite its relatively small size (914 hectares), Hastings has over one-third (27 of 75) of the Osmia species estimated in California by Moldenke & Neff (1974).

A comparison of our results with nine other North American surveys that include Osmia (Table 2) confirms the generalization that Osmia represent "boreal" species (Linsley 1958). The five most diverse Osmia locales (including Hastings) were at higher elevations (> 450 m) with substantial grassland/meadow components. The combined studies of Thorp et al. (1994) and Rust et al. (1985) yielded one-third as many Osmia species on Santa Cruz Island (off the coast of southern California) as in this survey, even though Hastings represents < 1% of the area

Table 1. A comparison of *Osmia* species collected during two study periods at the Hastings Natural History Reservation: 1937–43 and 1987–92.

	Collection period				
	-	1937–43		1987–92	
Species	Pres.*	(No., %)	Pres.*	(No., %)	
Osmia (Acanthosmioides) nifoata Cockerell		(7, 1.9)		(16, 2.7)	
Osmia (Centrosmia) bakeri Sandhouse	\circ	(0, 0.0)		(16, 2.7)	
Osmia (Cephalosmia) californica Cresson	0	(0, 0.0)		(4, 0.7)	
Osmia (Cephalosmia) montana Cresson		(15, 4.0)	\circ	(0, 0.0)	
Osmia (Chalcosmia) coloradensis Cresson		(2, 0.5)	\circ	(0, 0.0)	
Osmia (Chalcosmia) texana Cresson		(1, 0.3)		(30, 5.0)	
Osmia (Chenosmia) aglaia Sandhouse		(19, 5.0)		(65, 10.8)	
Osmia (Chenosmia) calla Cockerell		(2, 0.5)	\circ	(0, 0.0)	
Osmia (Chenosmia) clarescens Cockerell		(2, 0.5)	\circ	(0, 0.0)	
Osmia (Chenosmia) cyanopoda Cockerell	0	(0, 0.0)		(2, 0.3)	
Osmia (Chenosmia) granulosa Cockerell		(10, 2.7)		(9, 1.5)	
Osmia (Chenosmia) kincaidii Cockerell		(4, 1.1)		(5, 0.8)	
Osmia (Chenosmia) laeta Sandhouse		(12, 3.2)		(28, 4.7)	
Osmia (Chenosmia) pusilla Cresson		(1, 0.3)	\circ	(0, 0.0)	
Osmia (Chenosmia) regulina Cockerell		(29, 7.7)		(17, 2.8)	
Osmia (Chenosmia) trevoris Cockerell	0	(0, 0.0)		(5, 0.8)	
Osmia (Chenosmia) tristella Cockerell		(2, 0.5)		(6, 1.0)	
Osmia (Chenosmia) zephyros Sandhouse	0	(0, 0.0)		(7, 1.2)	
Osmia (Euthosmia) glauca (Fowler)		(193, 51.2)		(55, 9.1)	
Osmia (Monilosmia) albolateralis Sandhouse		(5, 1.3)		(2, 0.3)	
Osmia (Monilosmia) atrocyanea (Cockerell)		(8, 2.1)		(101, 16.8)	
Osmia (Monilosmia) brevis Cresson		(4, 1.1)		(8, 1.3)	
Osmia (Monilosmia) cara Cockerell		(1, 0.3)	\circ	(0, 0.0)	
Osmia (Monilosmia) cyanella Cockerell		(21, 5.6)		(41, 6.8)	
Osmia (Monilosmia) gabrielis Cockerell		(8, 2.1)		(13, 2.2)	
Osmia (Mystacosmia) nemoris Sandhouse	•	(21, 5.6)		(25, 4.2)	
Osmia (Osmia) lignaria Cresson		(8, 2.1)		(145, 24.1)	
Osmia (Osmia) ribifloris Michener	0	(0, 0.0)		(1, 0.2)	
Osmia (Trichinosmia) latisulcata Michener		(1, 0.3)	0	(0, 0.0)	
Osmia (Unassigned) claremontensis Michener	0	(0, 0.0)		(1, 0.2)	
Osmia undetermined specimens	_	(1, 0.3)		(0, 0.0)	
Totals	23	(377, 100.2)	23	(602, 100.2	

^{*} Species presence (●) or absence (○).

of the island. This result probably reflects the fact that Santa Cruz Island is species-poor relative to the mainland bee fauna (Thorp et al. 1994). The latitudinal extremes of Alaska (Armbruster & Gunn 1989) and Mexico (Ayala 1988) show little *Osmia* diversity as do the surveys conducted at Nevada and Utah sand dune habitats (Rust et al. 1983, Griswold, unpublished data).

Differences Between Surveys at Hastings.—Osmia lignaria Cresson was the most frequently collected species during the 1987–92 period (24% of the collection) while Osmia glauca was most common during the 1937–43 survey (193 of 377 specimens). All but one of the latter species were collected on the same day, 1 Jun, in 1938. Relatively few (eight) O. lignaria were collected during the early survey period, an artifact of a delayed initiation of the survey. The least common species in the current survey were. Osmia ribifloris and Osmia claremontensis

Table 2. A comparison of selected North American faunal surveys that include Osmia species.

Survey citation	Locale (disjunct sites) Habitat types	Years	Latitude	Elevation (m)	Method	No. subgenera Total (shared†)	No. spp. Total (shared†)
Armbruster & Gunn (1989)	USA—Alaska (32) variable–interior arctic	8	64.0–70.0° N	unreported	Net	2 (2)	4 (0)
Griswold (unpub.)	USA—Idaho (1) montane meadow	2	42.0–43.0° N	1768	Malaise	7 (7)	28 (13)
Tepedino (1982)	USA—Wyoming (2) shortgrass prairie	3	41.0–42.0° N	2250–2425	Net	7 (7)	20 (8)
Griswold (unpub.)	USA—California (4) montane meadow	3	40.0–41.0° N	1342–2286	Net	8 (7)	34 (17)
Griswold (unpub.)	USA—Nevada (5) montane meadow	3	40.0–41.0° N	2316–3109	Net	5 (5)	20 (7)
Rust et al. (1983)	USA—Nevada (2) sand dunes	2	39.0–40.0° N	1250–1400	Net	1 (1)	1 (0)
Griswold (unpub.)	USA—Utah (8) sand dunes	6	38.0-39.0° N	1372–1585	Net	5 (4)	7 (1)
Current study	USA—California (1) coastal foothill	10	36.0-37.0° N	467–953	Net	10 (-)	30 (-)
Thorp et al. (1994) ¹	USA—California (1) variable-island	5	33.5–34.5° N	0–753	Net	4 (4)	10 (9)
Ayala (1988)	MEX—Jalisco (1) seasonal lowland	5	19.0–20.0° N	unreported	Net	- (-)	0 (-)

¹ Based upon the work of Rust et al. (1985) which includes additional years of collections. † Number shared with current study.

whereas O. cara, O. pusilla, O. latisulcata and O. texana were the rarest of the original survey (all species represented by a single specimen). Fifteen species from the current survey were represented by ≤ 20 specimens, including all 7 species not recorded during the original collection period.

Although most species undetected between surveys were relatively rare or inconspicuous, the absence of O. coloradensis and O. montana in the recent survey is enigmatic. Both are well documented in California (Rust 1974) and are relatively large in size with a dark metallic appearance that makes them especially conspicuous to collectors. Both species prefer asteraceous pollen (Hurd 1979) and we have collected the closely related Osmia californica and Osmia texana from the thistle species Cirsium occidentale. Nectar sources such as Salvia mellifera and Vicia villosa were also monitored without encountering either Osmia (see Appendix). If either of these species were at Hastings during the current survey, they were in such low numbers as to be undetectable.

There may be several explanations for the apparent absence of species between survey periods. First, naturally occurring factors such as annual host plant variation could produce temporary declines in bee population levels. Bloom intensity of *Lupinus nanus* can vary 11-fold between years at Hastings, for example, potentially influencing those bee species that require its pollen (Knops & Barthell 1996). Population fluctuations may also reflect parsivoltinism, a condition in some *Osmia* species that delays emergence (Torchio & Tepedino 1982). The current survey was conducted during consecutive years, however, and we are likely to have encountered such species if they inhabited Hastings in high numbers.

Most plant species introductions occurred well before the first complete floral survey conducted at Hastings (Linsdale 1955). Knops et al. (1995), indicate that very early agricultural practices (≈ 1800s) have profoundly altered plant communities at Hastings. Over 28% of the grassland and 19% of the herbaceous communities, both important sources of host plants, are now alien species. How these long-term introductions have influenced *Osmia* is difficult to ascertain. Although bee species were collected from introduced host plants, most of these species were already at Hastings when the original survey was conducted.

Ten fires are known to have at least minimally affected Hastings in this century, seven since the reserve was established (Griffin 1988). In total, they affected \approx 206 hectares of the current reserve property and 88 ha (\approx 13%) of the original property. The extensive "Marble Cone" fire of 1977 did not reach Hastings but did alter nearby plant communities by producing an abundance of herbaceous species (Talley & Griffin 1980). This may have influenced pollen and nectar availability to bees, but there is no direct evidence of this occurring. Such fires also consume dead trees and limbs which might otherwise be used for nesting sites. There is little evidence that burns have had a serious effect on the availability of downed wood, however.

Species diversity has remained constant at Hastings between surveys (23 species) although cumulative species diversity has increased. Each survey had seven unique species, suggesting that species may become alternately present (detectable) and absent (undetectable) in the environment over time. The absence of conspicuous species such as *Osmia montana* and *Osmia coloradensis* in the most recent survey indicates that these absences are not necessarily an artifact of dif-

ferent collectors, underscoring the need for long-term surveys to better estimate species diversity.

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Appendix. Flower visitation records of Osmia species for which records are available.

Arbutus menziesii Pursh	Caprifoliaceae Lonicera interrupta Benth.	Brassicaceae Cardamine californica (Torrey & A. Gray) E. Greene	Boraginaceae Plagiobothrys nothofulvus (A. Gray) A. Gray	Asteraceae Centaurea melitensis L.* Cirsium occidentale (Nutt.) Jepson	Amaryllidaceae Triteleia ixoides (S. Watson) E. Greene	
0, +0	0, +0	0, +0	0, +0	0, +0 0, +0	0, +0	
11	1 1					O. (Acanth.) nifoata
11						O. (Centr.) bakeri
11				2		O. (Cephal.) californica
1.1				18+		O. (Chalc.) texana
1.1						O. (Chen.) aglaia
li i	1 1	1 1			1.1	O. (Chen.) cyanopoda
lii		, . 			ii	O. (Chen.) granulosa
lii			ii		ii 🛚	O. (Chen.) kincaidii
11				-		O. (Chen.) laeta
11				1 1 1 1		O. (Chen.) regulina
li i		1.1	1.1	1	1.1	O. (Chen.) trevoris
lii		1 1	1 1		1 1	O. (Chen.) tristella
lii	1 1		ii		ii	O. (Chen.) zephyros
11		1 1				O. (Euth.) glauca
11		11		1111		O. (Monil.) albolateralis
11	_	<u> </u>		1111		O. (Monil.) atrocyanea
				1111	1.1	O. (Monil.) brevis
					l <u>-</u>	O. (Monil.) cyanella
	11	1.1	1.1			O. (Monil.) gabrielis
	1					O. (Mystac.) nemoris
0			_			O. (Osmia) lignaria
-				1111		O. (Osmia) ribifloris
11				1.1.1.1		O. (None) claremontensis

Labiatae Rosmarinus sp.*	Hydrophylliaceae Pholistoma auritum (Lindley) Lilja Nemophila menziesii Hook. & Arn.	Fabaceae Lotus scoparius (Nutt.) Ottley Lupinus nanus Benth. Melilotus indica (L.) All.* Robinia pseudo-acacia L.* Trifolium sp. Vicia villosa Roth*	
O ₃ +O	O ₃ +O O ₃ +O	\$\phi\$ 1	O. (Acanth.) nifoata O. (Centr.) bakeri O. (Cephal.) californica O. (Chalc.) texana O. (Chen.) aglaia O. (Chen.) cyanopoda O. (Chen.) granulosa
		15† 12†	O. (Chen.) kincaidii O. (Chen.) laeta O. (Chen.) regulina O. (Chen.) trevoris O. (Chen.) tristella O. (Chen.) zephyros O. (Euth.) glauca O. (Monil.) albolateralis O. (Monil.) atrocyanea
		1 2 — — — — — — — — — — — — — — — — — —	O. (Monil.) alrocyanea O. (Monil.) brevis O. (Monil.) cyanella O. (Monil.) gabrielis O. (Mystac.) nemoris O. (Osmia) lignaria O. (Osmia) ribifloris O. (None) claremontensis

	Rhamnaceae Rhamnus californica Esch.	Polygonaceae Eriogonum fasciculatum Benth.	Oxalaceae <i>Oxalis pes-caprae</i> L.*	Onagraceae <i>Clarkia unguiculata</i> Lindley	Lamiaceae Marrubium vulgare L.* Salvia mellifera E. Greene* Stachys bullata Benth. Thymus sp.*	
	0, +0	0, +0	O ₃ +O	0, +0	0, +0 0, +0 0, +0 0, +0	
	1	1 1				O. (Acanth.) nifoata
	1 1					O. (Centr.) bakeri
١	11					O. (Cephal.) californica
١	11					O. (Chalc.) texana
	11			l <u>-</u>	25 5	O. (Chen.) aglaia
ı				1 1		O. (Chen.) cyanopoda
					6	O. (Chen.) granulosa
	11					O. (Chen.) kincaidii
			1 1	1 1	2 1	O. (Chen.) laeta
	I	1 1	1.1			O. (Chen.) regulina
		1 1	1.1	1.1		O. (Chen.) trevoris
			11	1 1		O. (Chen.) tristella
						O. (Chen.) zephyros
				$I \downarrow$		O. (Euth.) glauca
		11				O. (Monil.) albolateralis
		-			2	O. (Monil.) atrocyanea
				1.1	1 2	O. (Monil.) brevis
						O. (Monil.) cyanella
		1 1	1 1	1 1		O. (Monil.) gabrielis
						O. (Mystac.) nemoris
			- 17		1 25	
		1 1	7 -			O. (Osmia) lignaria O. (Osmia) ribifloris
						O. (None) claremontensis
i		1				o. (1 tollo) ciul emoluelists

Violaceae Viola pedunculata Torrey & A. Gray	Verbenaceae	Scrophulaceae	Rosaceae
	Verbena lasiostachys Link	Collinsia heterophylla Buist	<i>Cydonia</i> sp.*
\$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	\$\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\

- O. (Acanth.) nifoata
- O. (Centr.) bakeri
- O. (Cephal.) californica
- O. (Chalc.) texana
- O. (Chen.) aglaia
- O. (Chen.) cyanopoda
- O. (Chen.) granulosa
- O. (Chen.) kincaidii
- O. (Chen.) laeta
- O. (Chen.) regulina
- O. (Chen.) trevoris
- O. (Chen.) tristella
- O. (Chen.) zephyros
- O. (Euth.) glauca
- O. (Monil.) albolateralis
- O. (Monil.) atrocyanea
- O. (Monil.) brevis
- O. (Monil.) cyanella
- O. (Monil.) gabrielis
- O. (Mystac.) nemoris
- O. (Osmia) lignaria
- O. (Osmia) ribifloris
- O. (None) claremontensis

* Introduced plant species. † Confirmed pollen source

_" = no records.